

THE SKULL OF *STRUTHIOCEPHALUS KITCHINGI*

By

LIEUWE DIRK BOONSTRA

South African Museum, Cape Town

(with 11 figures in the text)

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INTRODUCTION

Since Brink's description in 1958 of the type skull (B.P.I. 284) found on De Bad, Beaufort West by Kitching, the author with H. Zinn and H. Boonstra had the good fortune to excavate a second skull (S.A.M. K272) on Perdefontein, Beaufort West in 1960.

This skull was found *in situ* lying upside down with parts of the lower jaws exposed and the rest intact in a mudstone matrix. Unfortunately the exposed lower jaws have suffered from weathering which has destroyed the posterior parts of both rami. The palatal surface of the skull was firmly encased in a jacket of reinforced plaster and the massive skull could be lifted in one piece. On preparation the skull proved to be very well preserved and only very slightly distorted.

On study it became apparent that this specimen shows a number of structural features much better than the type specimen does. Certain additions to Brink's description can thus be made and in the sequel it will also become clear that I differ in interpretation on a number of points, even if allowance is made for considerable individual variation.

A correction has also to be made in regard to the type species due to Brink having misread Broom. The species *whaitsi* has as its holotype the skull (S.A.M. 2678) from Vivier, Beaufort West and the second specimen mentioned by Broom consists of a skull and much of the skeleton (S.A.M. 3012) from Abrahamskraal, Prince Albert. Broom rightly thought that the second specimen belonged to the same species as the holotype skull. There are thus two skulls and one skeleton.

DESCRIPTION

Build and carriage of the skull

The fronto-nasal boss in my specimen is very like that of the type, but I do not think that it represents a horn-core. In the collection of the South African Museum there are over two dozen skulls of *Struthiocephalus* and *Keratocephalus*. These all have a fronto-nasal boss developed to a varying degree and in all of them the sculpturing of the boss is very similar to that of the skull in general. If the boss were a horn-core one would have expected its surface to differ from that of the general skull sculpturing. That the boss could have been used as a battering ram is most probable, but then without a special horn covering.

There is no doubt about the hang-dog carriage of the skull in *Struthiocephalus*. As a matter of fact this applies to all the tapinocephalians in general—also to those without a naso-frontal boss. The struthiocephalines, with their long snouts and anteriorly directed upper front teeth, undoubtedly fed on softer vegetable matter than the moschopines. Their limbs have also been shown to be more adapted to marshy conditions and Brink's suggestion that the struthiocephalines may even have fed duck-like under water is quite probable. The surface moulding of the bone around the nostrils—especially of the septomaxilla—suggests the presence of musculature for the closing off of the nostril.

The structure of the skull

Although the present skull is very well preserved and prepared a number of sutures cannot be traced with absolute certainty. This is due to a number of factors such as the rugose nature of the outer surfaces, closure of sutures, fusion of elements and small displacements. When comparing the figures given here with those of the type skull, and also with those of other species of the genus the effects of the pachyostosis should be born in mind. The pachyostosis in the tapinocephalians is to some extent individual with differences often seen between the relations and extent of the two bones of a pair in the same skull. Age is also a factor. Differences that have been given as specific are often due to differences in the tempo of the pachyostosis in adjoining bones. Thus a strong pachyostotic development in, for instance, the postfrontal, causes an overlap or overgrowth over the adjoining bones and affects the relative size and shape of the outer surfaces of these bones. Where, however, authors show a radical difference in the relations of bones errors of observation and/or interpretation must be considered probable.

Lateral and dorsal surfaces. (Figs. 1 and 2)

In comparing my figures with those of Brink it is manifest that the type skull has been subjected to dorso-ventral compression. The effects are especially obvious in the nature and disposition of the lateral pterygoid flange and the

quadrate. It should, moreover, be borne in mind that my figures are ortho-projections and not perspective drawings. This would in part account for the fact that in my figures the tabular is visible in dorsal view and in lateral view forms much of the posttemporal bar. But in my specimen the tabular is really much more developed and in its forward growth overlaps much of the lateral

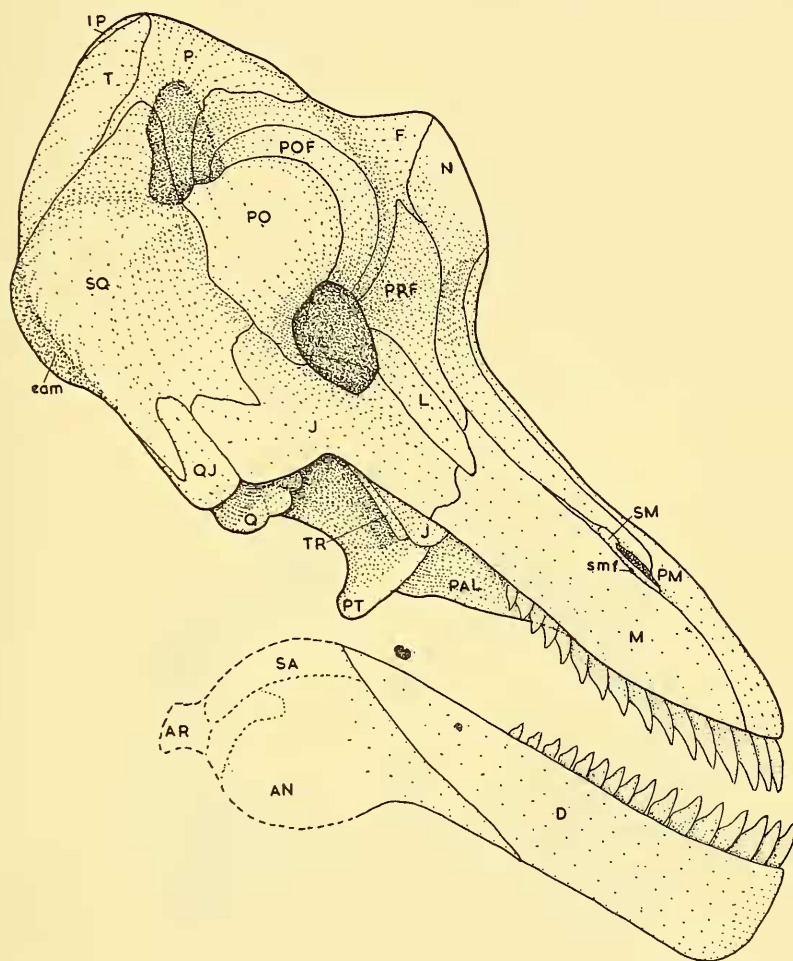


FIG. 1. *Struthiocephalus kitchingi*. S.A.M. K272 $\times 1/6$. Lateral view. Orthoprojection on to the sagittal plane.

AN—angular. AR—articular. D—dentale. eam—external auditory meatus. F—frontal. IP—inter- or postparietal (dermo-supraoccipital). J—jugal. L—lacrima. M—maxilla. N—nasal. P—parietal. PAL—palatine. PM—premaxilla. PO—postorbital. POF—postfrontal. PRF—prefrontal. PT—pterygoid. Q—quadrate. QJ—quadratojugal. SA—surangular. SM—septomaxilla. smf—septomaxillary foramen. SQ—squamosal. T—tabular. TR—transversum (ectopterygoid).

tongue of the parietal which is wedged in between the tabular and the upsweeping process of the squamosal. In my specimen the postorbital is more developed and this at the expense of the postfrontal. This particularly affects the appearance of the postorbital bar as seen in dorsal view.

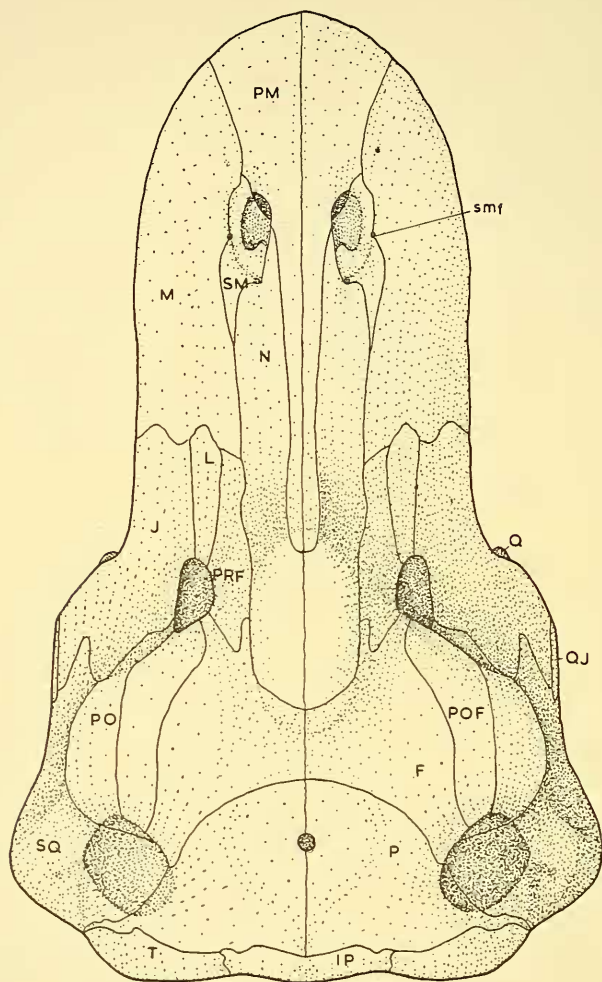


FIG. 2. *Struthiocephalus kitchingi*. S.A.M. K272 $\times 1/6$. Dorsal view.
Orthoprojection on to the alveolar plane.

Brink figures the squamosal as entering the ventral orbital border, whereas in my specimen the jugal extends posteriorly, ventral to the postorbital and forms nearly all of the ventral rim of the orbit with a small contribution by the postorbital. This is the normal relation, not only in the tapinocephalids

but also in all the other Dinocephalia (anteosaurids, titanosuchids, styraccephalids and the Russian brithopids). Brink's figure indicates an error in observation.

In the present specimen the outer surface of both septomaxillaries is well preserved and this shows a distinctive moulding of the posterior border of the nostril to form a rounded swollen rim set off by the presence of a lateral groove. I suggest that this moulded structure indicates attachments for a valvular closure of the nostril when the animal is feeding with the snout submerged.

Occiput. (Fig. 3)

The occiput is low and broad with the squamosals bulging laterally to form prominent 'cheeks'. A strong rounded thickened upper and lateral border formed by the interparietal and the tabulars prominently demarcates a deep bipartite area of origin for the nuchal muscles. The interparietal and the tabulars have large posterior faces, whereas the supraoccipital is very low. The large face of the paroccipital is directed much more ventrally than posteriorly. The ridge on the squamosal bounding the external auditory meatus medially is very prominent. The posttemporal fossa is all but closed by the downgrowth

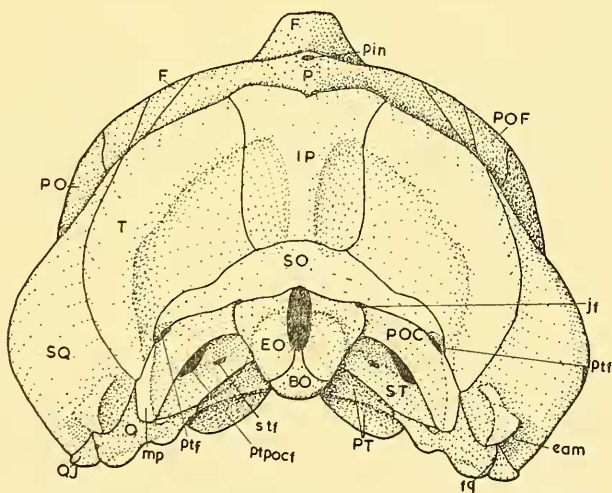


FIG. 3. *Struthiocephalus kitchingi*. S.A.M. K272 $\times 1/6$. Occipital view. Orthoprojection at right angles to the sagittal and alveolar planes.

BO—basioccipital. EO—exoccipital. fq—quadrate foramen. jf—jugular foramen. mp—mastoid process of the paroccipital. pin—pineal (parietal) foramen. POC—paroccipital. ptf—posttemporal fenestra. ptpocf—pterygo-paroccipital fenestra. SO—supraoccipital. ST—stapes. stf—stapedial foramen.

Other lettering as for Fig. 1.

of the tabular. The stapes is seen to lie diagonally with the distal end lying low down in the recess on the quadrate. Little is seen of the posterior face of the quadrate in this view because of its horizontal disposition. The occipital condyle is directed much ventrally with the exoccipitals forming most of the posterior face and the basioccipital facing mainly ventrally.

Ventral surface. (Fig. 4)

Comparing my figure of the ventral surface to that given by Brink a number of differences are apparent, apart from the fact that mine is a projection and Brink's a perspective drawing. The differences are in main due to the fact that the present specimen being uneroded is in a much better state of preservation. The regions mainly affected are the transverse processes of the pterygoids, quadrate and stapes, the occipital condyle and the relations of the supraoccipital, interparietal, tabular and squamosal.

In the present specimen the lateral flanges of the pterygoids form well demarcated deep transverse ridges extending far ventrally in their lateral parts, lying far below the level of the quadrate rami.

In its lateral part the quadrate ramus forms a deep vertical flange of bone which meets the quadrate along a large synchondrotic face. More medially the pterygoid is deeply vaulted and sends a process posteriorly which abuts against the paroccipital at a level higher than the quadrate process of the paroccipital.

The quadrates are well preserved and carry cotyli shaped as shown in the figure. The stapedia recess is well preserved on both sides.

Both stapes are well preserved and are seen to lie diagonally with the distal ends lying well anterior to the plane of the fenestrae ovals. The occipital condyle is a prominent large knob roughly circular in outline with its articular face directed only slightly posterior off the ventral. The exoccipitals form more of the articular face than is shown in Brink's figure.

The paroccipital has a large ventral face. Medio-anteriorly it has a process meeting the proötic above the level of the fenestra ovalis. Latero-anteriorly there is a long quadrate process applied to the quadrate and terminating posterior to the stapedia recess. At a higher level the quadrate process of the paroccipital has a thin flange of bone whose anterior edge meets a process of the quadrate ramus of the pterygoid. Posterolaterally the paroccipital develops an everted thickened edge underlying the squamosal to form a mastoid process. The supraoccipital is wide but low and the posttemporal fossa all but obliterated by the overgrowth of the large paroccipital. The tabular has a large ventral face which, however, does not extend anteriorly between the paroccipital and squamosal as shown by Brink in his figure of the type.

The squamosal carries a prominent ridge, roughly comma-shaped in outline, and this forms the internal limit of the external auditory meatus developed as an antero-posteriorly directed groove.

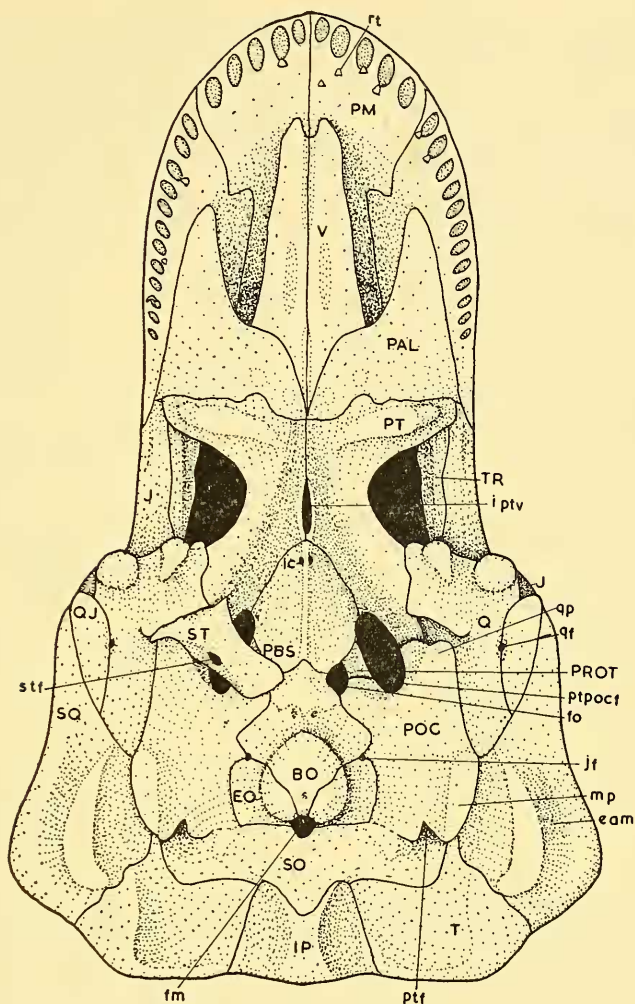


FIG. 4. *Struthiocephalus kitchingi*. S.A.M. K272 $\times 1/6$. Ventral view. Orthoprojection on to the alveolar plane.
 fm—foramen magnum. fo—fenestra ovalis. ic—internal carotid foramina. iptv—interpterygoid vacuity. PBS—parabasisphenoid. PROT—prootic. qp—quadrate process of the paroccipital. rt—replacing teeth. V—vomer. Other lettering as in previous figures.

The position of the stapes. (Fig. 5)

In order to describe the relations of the stapes to the bones with which it makes contact I have sketched the various bones disarticulated but lying in their relative positions.

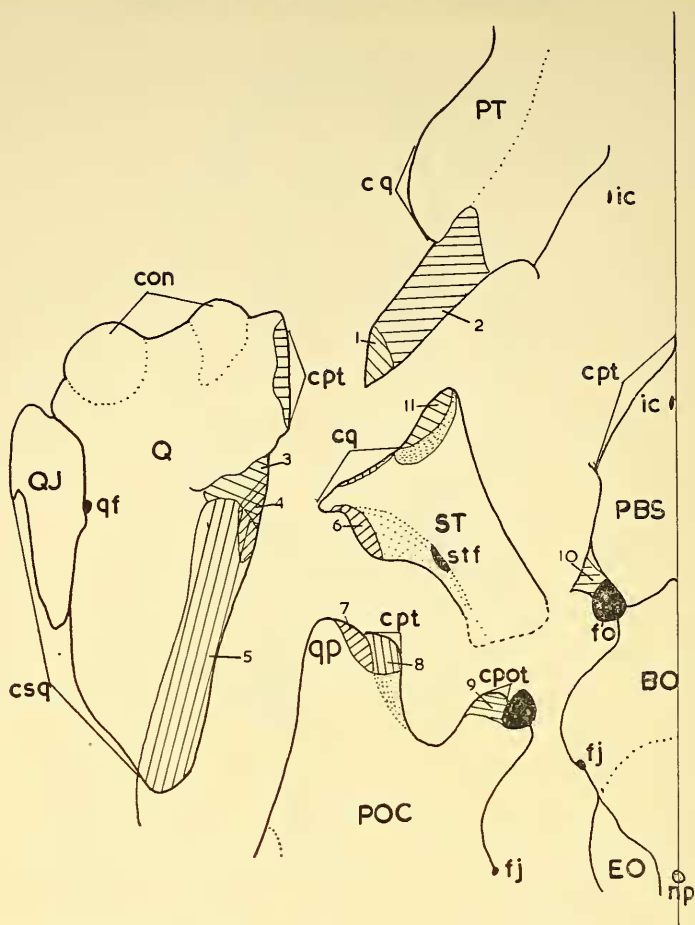


FIG. 5. *Struthiocephalus kitchingi*. S.A.M. K272 $\times 1/3$. The stapes and contiguous bones as disarticulated. Ventral view. Orthoprojection on to the alveolar plane.

con—condyles of the quadrate. cpt—contact of pterygoid (quadrate ramus) with the quadrate, paroccipital and para-basisphenoid. cpot—contact of paroccipital with the proötic. cq—contact of quadrate with the pterygoid and the stapes. csq—contact of the squamosal with the quadrate and the quadratojugal. np—notochordal pit in the basioccipital.

Other lettering as in previous figures.

- 1—wedge of the pterygoid applied to the medial edge of the quadrate (4).
- 2—area on the posterior process of the quadrate ramus of the pterygoid overlapping the distal end of the stapes.
- 3—surface of the quadrate overlapping the stapes dorsal to the stapedia recess proper.
- 4—area on the medial edge of the quadrate making contact with the posterior process of the quadrate ramus of the pterygoid.
- 5—surface of the quadrate underlapped by the paroccipital.
- 6—area on the dorsal process of the stapes in contact with the paroccipital (7).
- 7—area on the paroccipital in contact with the dorsal process of the stapes (6).
- 8—area on the paroccipital underlapped by the stapes.
- 9—area on the paroccipital underlapped by the proximal end of the stapes.
- 10—area of the proötic underlapped by the stapes.
- 11—hollow in the distal end of the stapes which receives a process of the quadrate.

The footplate of the stapes lies fitted into the fenestra ovalis on both sides so that its proximal end cannot be seen.

Antero-dorsally the proximal end of the stapes is applied to a face on the proötic and further posteriorly underlies a face on the paroccipital. Both these contacts are not very intimate—definitely not synostotic—but rather syndesmotic or synchondrotic. Ventrally the footplate is in contact with the edges of the fenestra ovalis formed by the paroccipital, basioccipital and the para-basisphenoid.

The distal end of the stapes makes contact with the quadrate and paroccipital.

Postero-laterally the distal end of the stapes has a fairly short truncated process—the tympanic process—whose tip is connected directly or by the intercalation of a cartilaginous extra-stapes to the tympanum.

Antero-medially of this tip the distal end of the stapes fits into an elongated groove-like stapedial recess in the quadrate, lying in a plane nearly parallel to the quadratic cotyli. The fit is not tight and movement in this diagonal plane is possible even with the presence of cartilage or connective tissue.

The anterior part of the distal surface of the stapes has an oval hollowed-out articulatory face which makes contact with a process of the quadrate lying anterior to the elongated stapedial recess and posterior to the surface of contact with the end of the quadrate process of the pterygoid.

On the postero-distal surface of the stapes, posterior and medial to the tympanic process, and at a higher level than the main shaft of the stapes lies the dorsal process of the stapes, which makes contact with the quadrate process of the paroccipital. This contact was apparently synchondrotic.

Stapes. (Fig. 6)

In ventral view the stapes presents a main portion consisting of a proximal end forming the footplate, a greatly expanded distal end and a shaft with a waist-like constriction. From the posterior edge of this main portion the rest of the bone lies at a higher level. About halfway along the shaft a large oval stapedial foramen pierces this flange. Postero-distally of the foramen there is a process which meets the paroccipital—this is the dorsal process.

The distal end bears a process directed postero-distally—this is the tympanic process. Anterior to the tip of the tympanic process the distal end has an elongated face which fits into the stapedial recess in the quadrate.

Anterior to this the distal end presents a concave oval articulating face, which articulates with a convex process on the quadrate lying immediately posterior to the contact face on the quadrate, which receives the quadrate process of the pterygoid.

In dorsal view the stapes has the surface of its main portion and the surface of the dorsal process lying in the same plane. On the upper face of the dorsal process there rises a conical protuberance with its tip directed medially. This I have labelled the medial dorsal process. The function of this process

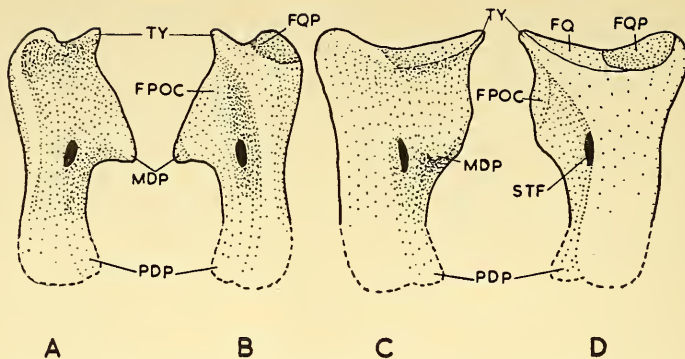


FIG. 6. Right stapes of *Struthiocephalus kitchingi*. S.A.M. K272 $\times 1/3$. A—anterior. B—posterior. C—dorsal. D—ventral. FPOC—facet on the dorsal process which is applied to the quadrate process of the paroccipital. FQ—facet fitting into the elongated stapedial recess in the quadrate. FQP—concave facet applied to a convex process on the quadrate lying medial to the stapedial process proper. MDP—medial dorsal process. PDP—proximal dorsal process. STF—stapedial foramen. TY—tympanic process.

would appear to be to receive a tendon probably attached to the inner edge of the quadrate.

In anterior and posterior view this median dorsal process is seen to be both strong and prominent.

Quadrate. (Fig. 7)

The quadrate is a large bone—robust in its cotylar region and in the parts making contact with the squamosal, quadratojugal and the quadrate ramus of the pterygoid. But its inner portion overlying the paroccipital consists of a thin sheet of bone with a free edge.

Its stout pterygoid process bears a large roughly oval area for the reception of the quadrate ramus of the pterygoid, which at a higher level has an additional process meeting the quadrate in a groove on the lower part of the inner edge of the quadrate. The articulatory area on the pterygoid process is a hollowed out area with, in its middle part, a longitudinal ridge. This is matched on the quadrate ramus of the pterygoid by an articulating face bearing a median groove flanked by two longitudinal ridges.

The nature of this joint is such that it admits of movement between the quadrate and the pterygoid in a parasagittal plane. The roughness of both articulating faces indicates the presence of synchondrotic cartilage.

Just above the quadrate-ptyerygoid articulation there is a transverse everted flange of bone. The upper edge of this flange carries a transverse groove which thus lies between two lips. This groove is the stapedial recess. The outer end of this everted flange develops a thin free standing process to which the tympanum was probably attached.

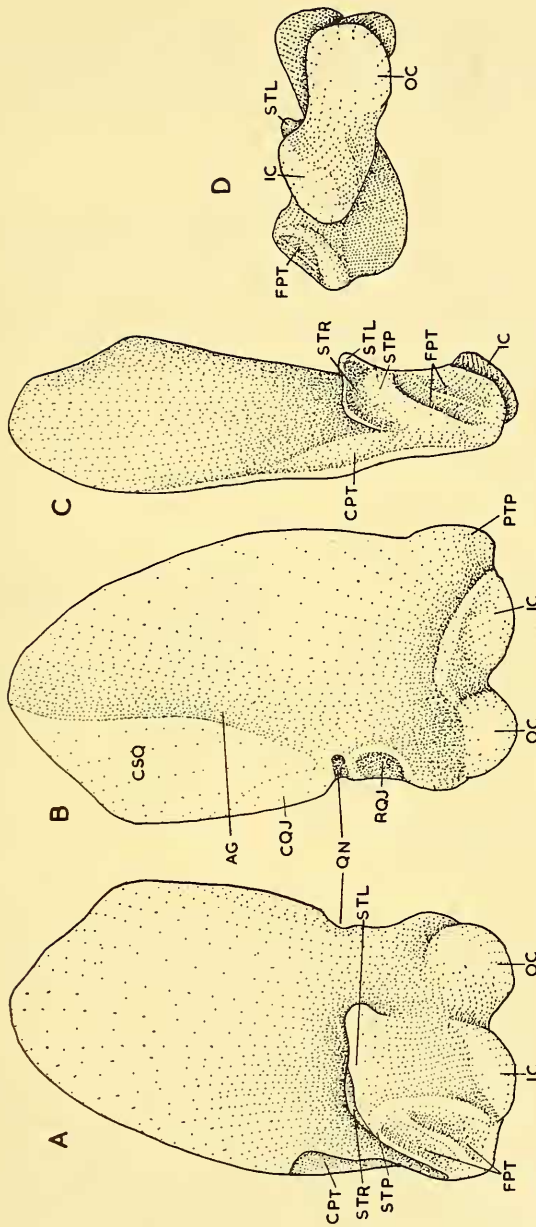


FIG. 7. Right quadrate of *Struthiocephalus kitchingi*. S.A.M. K272 $\times 1/3$.

A—ventral (morphologically posterior). B—dorsal (morphologically anterior). C—inner or medial. D—anterior (morphologically ventral). AG—groove in dorsal (anterior) surface housing part of the m. capiti-mandibularis. CPT—surface on the medial edge of the quadrate receiving the posterior process of the quadrate ramus of the pterygoid. CPT—surface of contact with the quadratojugal. CSQ—surface for contact with the squamosal. FPT—facet on the pterygoid process of the quadrate receiving the quadrate ramus of the pterygoid. IC—internal condyle. OC—external condyle. PTP—pterygoid process of the quadrate. QN—notch forming the inner border of the quadrate foramen. RQJ—recess receiving the ventral end of the quadratojugal. STL—ledge forming the posterior lip of the stapedial recess. STP—convex process for articulation with the concave facet on the distal end of the stapes. STR—the elongated recess for the reception of the stapes (stapedial recess proper).

In between the quadrate-pterygoid joint and the outer lip the everted flange has a rounded process to which is articulated the hollow face on the distal end of the stapes.

On its posterior face the quadrate is greatly thickened where it is applied to the squamosal and quadratojugal. Medial to this thickened area lies a wide groove with a smooth surface. This housed part of the body of the m. capitimandibularis.

A moschopid and jonkeriid quadrate. (Figs. 8 and 9)

I am including comparable figures of a quadrate of a moschopid and a jonkeriid. Essentially these are of the same type as that of *Struthiocephalus*, except that in the jonkeriid quadrate a very definite recess is developed on the posterior face well above the stapedial recess. I can offer no suggestion as to what was received in this recess.

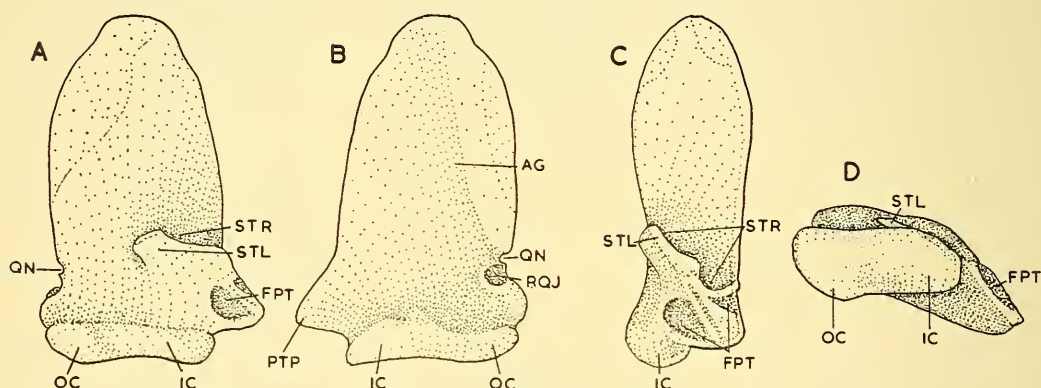


FIG. 8. Left quadrate of *Moschops* sp. S.A.M. 11701 $\times 1/3$.

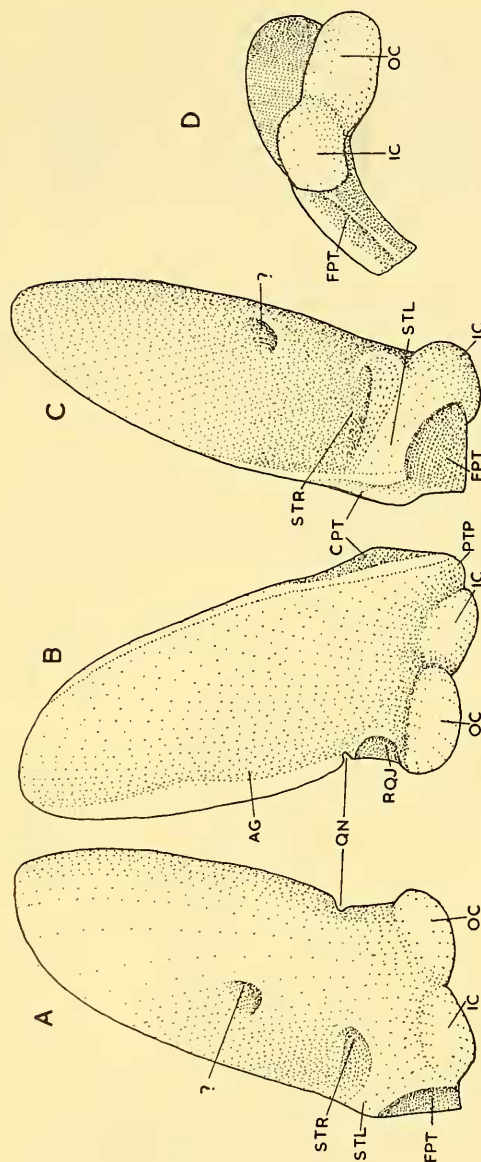
The Tympanum

A depressor mandibuli muscle originating from the prominent ridge on the squamosal just medial of the groove housing the external auditory meatus and inserted on the process of the articular would allow ample room for a tympanum with a diameter of about 30 mm.

The tympanum having one point of attachment on the free tip of the lip of the ledge bounding the stapedial recess could lie in a parasagittal plane and receive the tympanic process of the stapes meeting it at right angles.

The external auditory meatus extending from the tympanum along the groove in the posterior face of the squamosal could have its opening just above the level of the upper limit of the squamosal ridge.

The nature of the joint of the stapes with the quadrate as described above would allow of movement of sufficient amplitude for the conduction of sound waves.

FIG. 9. Right quadrate of *Jonkeria haughtoni*. S.A.M. 4343 $\times 1/3$.*Dentition.* (Fig. 10)

Brink maintains that in the type specimen the marginal teeth are disposed in a double row both functional at the same time. This view is manifestly incorrect. The fact is that the replacing teeth arise lingually of those in use and each new tooth is thus a younger member of the same tooth family of

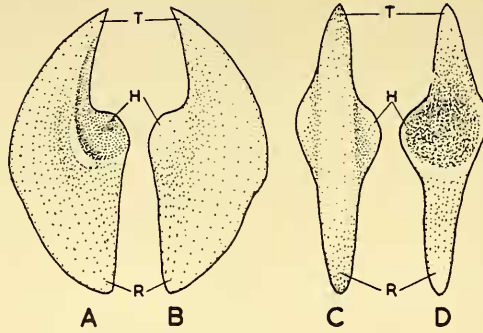


FIG. 10. First left incisor of *Struthiocephalus kitchingi*.

S.A.M. K272 $\times \frac{1}{2}$.

A—posterior. B—anterior. C—labial view.
D—lingual view. H—heel. R—root. T—talon.

the tooth it replaces. The position is thus as in the *Titanosuchia*. The structure of the teeth is of the talon-and-heel type throughout the series, with decrease in size in posterior direction.

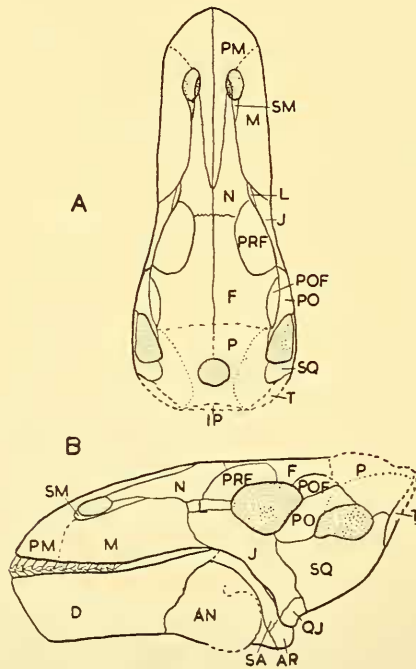


FIG. 11. Skull of *Moschosaurus longiceps*. Type.

S.A.M. 3015 $\times \frac{1}{6}$.

A—dorsal. B—lateral.

DISCUSSION

In a recent paper I have suggested that all the described species of *Struthiocephalus* could well be considered conspecific and I arranged them in a growth series.

I would now go further and suggest that *Moschosaurus* could very well be the youngest form of such a series. (Fig. 11)

SUMMARY

A detailed description of the skull of *Struthiocephalus kitchingi* is given, based on a second skull from Beaufort West. This specimen shows a number of features much better than the type specimen and leads to some differences in interpretation.

ACKNOWLEDGEMENTS

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